

Intraguild predation by *Tupiocoris cucurbitaceus* on *Encarsia formosa* and its influence on biological control of *Trialeurodes vaporariorum*

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Abstract

The predator *Tupiocoris cucurbitaceus* (Spinola) and the parasitoid *Encarsia formosa* Gahan are natural enemies of *Trialeurodes vaporariorum* (Westwood) that can be found simultaneously in greenhouse tomato crops. Whether or not these species are involved in a trophic interaction with each other, and how this interaction might impact the control of the whitefly population has not been explored so far. In the present study, we evaluate the consumption and preference of *T. cucurbitaceus* for parasitized and non-parasitized *T. vaporariorum* nymphs. Furthermore, the effect that the joint presence of both natural enemies can have on the control of the whitefly population. Our results show that under laboratory conditions *T. cucurbitaceus* females engage in intraguild predation on *E. formosa* pupae. However, given the choice, the predator prefers to prey on healthy *T. vaporariorum* nymphs. Under greenhouse conditions, however, both *T. cucurbitaceus* and *E. formosa* reduce whitefly population when released separately, and their control is enhanced when released together.

Key words: biological control, *Tupiocoris cucurbitaceus*, *Encarsia formosa*, tomato, pests.

Introduction

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) is one of the most important pests of tomato crops in Argentina. The main strategy employed to control this pest is the use of insecticides which often result in the development of resistance, especially when used in confined environments such as greenhouses (Gorman *et al.*, 2007; Erdogan *et al.*, 2021), leading to more frequent applications. This exacerbated use of pesticides has negative effects on human health, increases residues in crops and is unfriendly to the environment in general, affecting not only beneficial species, such as natural enemies, but also polluting the air, soil and water (Pimentel and Burgess, 2014). In recent years, the application of biological control approaches that promote the use and conservation of natural enemies in agroecosystems, in an integrated pest management context, has gained interest in Argentina.

Tupiocoris cucurbitaceus (Spinola) (Hemiptera Miridae) is a generalist predator found in several American countries: Canada, USA, Mexico, Costa Rica, Panama, Colombia, Ecuador, Brazil, Peru, Chile, Argentina and Uruguay (Carvalho, 1947; Carvalho and Ferreira, 1972; Carvalho and Afonso, 1977). In Argentina, it is present extensively (from 23°S to 43°S) and on a variety of host plants including wild and cultivated Geraniaceae, Rosaceae, Compositae, Fabaceae and Cucurbitaceae species, having a preference for Solanaceae species (Carpintero and Carvalho, 1993; Carpintero, 1998; 2004). In particular, this predator is usually found preying on the greenhouse whitefly *T. vaporariorum* on tomato, where it has a well-documented potential as biocontrol agent (López *et al.*, 2012; 2019; Orozco Muñoz *et al.*, 2012). Currently, in Argentina *T. cucurbitaceus* is commercially used in integrated pest management strategies to control whiteflies along with other tactics, such as the use of specific low residual power

insecticides compatible with the predator (Polack *et al.*, 2017). Besides, in laboratory assays, it has shown predation on several tomato pests, such as *Tuta absoluta* (Meyrick) (Lepidoptera Gelechiidae), *Myzus persicae* Sulzer (Hemiptera Aphididae) and *Tetranychus urticae* Koch (Acarina Tetranychidae) (López *et al.*, 2019; Cagnotti *et al.*, 2021; Cuello and López, 2021). *T. cucurbitaceus* is predominantly a predator and although phytophagy can occur in the young nymphal stages, it does not satisfy the food requirement for development and reproduction (Orozco Muñoz *et al.*, 2012). The aphelinid parasitoid *Encarsia formosa* Gahan (Hymenoptera Aphelinidae) is another natural enemy of *T. vaporariorum* whose presence in tomato crops is frequently spontaneous (Polack *et al.*, 2017) although it is not used commercially. The joint presence of both natural enemies can have different effects on the control of pest population if, in addition to sharing prey, they engage in a trophic interaction with each other (Rosenheim *et al.*, 1995).

Intraguild predation (IGP) is a widespread interaction within communities of natural systems and agroecosystems (Jansen *et al.*, 2006). It occurs when two potential competitors that share a resource or prey species, are involved in predator-prey interactions with each other (Polis *et al.*, 1989). When predators and parasitoids are involved in IGP, the interaction is unidirectional, either because the predator feeds directly on the parasitoid (for example, predated the free-living adult stage) or indirectly, by feeding on the parasitized prey, consuming both the host and the associated immature parasitoid (Rosenheim *et al.*, 1995). This kind of interaction can have an important influence on the regulation of a pest population. Depending on the efficiency and preference of the predator for the type of prey (parasitized or non-parasitized), the results of the biological control strategy can be harmful, beneficial or null (Colfer and Rosenheim, 2001). Several studies show that

in whitefly-predator-parasitoid systems, predators are capable of feeding on immature and even adult stages of the parasitoids with no negative effect over the pest control (Malo *et al.*, 2012; Al-Zyoud, 2014; Velazco-Hernández *et al.*, 2014; Bao-Fundora *et al.*, 2016).

The system *T. vaporariorum*-*T. cucurbitaceus*-*E. formosa* is found in tomato crops under greenhouse conditions in Argentina. However, the outcome of this interaction and its effect on the biological control of whiteflies have not been explored so far. In the present study, we evaluate the consumption and preference of *T. cucurbitaceus* for parasitized and non-parasitized *T. vaporariorum* nymphs and the effect of the joint presence of both natural enemies on the biological control of the greenhouse whitefly. Our hypothesis is that *T. cucurbitaceus* feeds on both types of prey (parasitized and non-parasitized whitefly nymphs) and that predation on *E. formosa* pupae has a negative impact on the biological control of *T. vaporariorum* when both natural enemies are introduced together.

Materials and methods

Insects

The whiteflies used in the experiments were part of a colony maintained in our laboratory in a climate-controlled room at 25 ± 2 °C, RH 50-80% and 14L: 10D photoperiod.

To obtain non-parasitized whitefly nymphs, tomato plants were exposed to *T. vaporariorum* adults isolated in clip-cages on individual leaflets. After 24 hours exposure, adults were removed and plants held in enclosure cages (0.80 m high by 0.55 m wide by 0.60 m long) covered with fine-mesh cotton organdie until the nymphs reached the fourth instar stage, used in the experiments.

To obtain the *E. formosa* pupae, tomato leaflets infested with whitefly nymphs about 14 days old were exposed to five adults of the parasitoid from our laboratory rearing, inside a clip-cage. After 24 hours exposure, parasitoids were removed and host nymphs were kept in a climate controlled room under similar environmental conditions until parasitoid progeny were observed pupating. This stage of the parasitoid, used in the experiments, is recognizable by the change in colour, from white to black, of the host cuticle.

Female adults of *T. cucurbitaceus* were obtained from our laboratory cultures reared on tomato and tobacco plants and fed on *Sitotroga cerealella* (Olivier) (Lepidoptera Gelechiidae), also reared in our laboratory, and *Artemia* sp. eggs commercially acquired. This long-standing colony of the predator is kept inside a climate controlled room at 25 ± 3 °C, $65 \pm 15\%$ RH and 14L:10D photoperiod, and augmented every spring-summer with field populations from local greenhouses.

Non-choice experiment

To estimate *T. cucurbitaceus* consumption levels on non-parasitized and parasitized whiteflies, fourth instar nymphs of *T. vaporariorum* and *E. formosa* pupae were offered to predator adult females. The experimental arena consisted in a Petri dish (5 cm diameter, 1 cm high) with

a tomato leaflet ($\sim 3 \times 2$ cm) sustaining one type of prey, leaning on a moistened filter paper. After 24 hours of starvation, in which mirids were only given water, *T. cucurbitaceus* females ($n = 15$) were individually exposed to 60 non-parasitized or 60 parasitized whiteflies (López *et al.*, 2019) and allowed to forage in the arena for 24 hours.

The number of consumed fourth instar whiteflies was recorded using a stereoscopic microscope, by counting the empty cuticle or bodies partly emptied.

In the case of parasitized whiteflies, identifying the consumption level is not straightforward. In this case, the experimental arenas containing *E. formosa* pupae were kept in a climatic chamber (25 ± 3 °C, $65 \pm 15\%$ RH and 14L:10D) until adult emergence. Mortality of *E. formosa* pupae was corrected with that in the control treatment without presence of the predator ($n = 15$). Previous studies (López *et al.*, 2019) showed that the mortality of fourth instar whitefly nymphs in 24 hours is negligible, so this control experiment was not performed.

Free-choice experiment

We followed the same experimental procedure described for the non-choice experiment except that predators were offered both preys simultaneously. The experimental arena consisted in two tomato leaflets, one with 30 fourth instar whiteflies and the other with 30 pupal stage parasitoids offered to predatory mature females ($n = 15$). The number of consumed whitefly nymphs was registered after 24 hours exposure. As in the non-choice experiments, *E. formosa* pupae were kept in a climatic chamber until adult emergence and compared with the control treatment (30 *E. formosa* pupae without the predator).

Greenhouse experiment

The experiment was carried out inside a greenhouse (7.10×4.55 m), with no artificial light source or climate control, belonging to the Insectario de Investigaciones Lucha Biológica at INTA Castelar, Buenos Aires province, Argentina. Temperature and humidity were registered daily with a thermohygrometer placed in the middle of the greenhouse. Twenty cages ($1 \times 0.7 \times 1.2$ m) were placed inside the greenhouse, covered with a fine-mesh cotton organdie. Each cage enclosed six potted tomato plants (*Solanum lycopersicum* L. var. *platense*), 50 cm tall with 6-8 leaves and in a flowering state at the beginning of the experiment. At the end of the experiment tomato plants were in a state of fruit development. Thirty *T. vaporariorum* adults were introduced in each cage. After two weeks, to allow whiteflies establishment, cages were randomly assigned to one of four treatments: 'control', whiteflies alone; 'Te', whiteflies + *T. cucurbitaceus* adults (4 females + 2 males); 'Ef', whiteflies + *E. formosa* (6 adults); and 'combined', whiteflies + *T. cucurbitaceus* (4 females + 2 males) + *E. formosa* (6 adults). The number of natural enemies released corresponds to the commercially recommended doses. Once a week, from March 30th until May 26th 2022 (9 weeks), the number of fourth instar nymph whiteflies and *E. formosa* pupae were counted in two randomly selected leaves (one from the top and one from the middle of the plant) while *T. cucurbitaceus* nymphs and adults were counted in the entire plants. *T. vaporariorum* and *E. formosa* were reintroduced twice into the cages -

the previous week to the beginning of the evaluations and after the first counting date together with *T. cucurbitaceus* adults. In all cases the initial doses were employed. In the treatments where *T. cucurbitaceus* was released, *Artemia* sp. eggs were added as supplementary food only at its first release in order to ensure the predator establishment. Observations were made by a hand-held 10× magnifier.

Data analysis

Non-choice experiment

The number of consumed preys was corrected by the mortality obtained in the controls through the application of the Abbott formula (Abbott, 1925). Differences in consumption levels of the predator between *T. vaporariorum* fourth instar nymphs and *E. formosa* pupae were analysed with a one way ANOVA using InfoStat (Di Rienzo *et al.*, 2015).

Free-choice experiment

The number of consumed preys was corrected by the mortality obtained in the controls through the application of the Abbott formula (Abbott, 1925). Differences in consumption of the predator between *T. vaporariorum* fourth instar nymphs and *E. formosa* pupae were analysed with a *t* test for paired samples using InfoStat (Di Rienzo *et al.*, 2015). Predator preference was analysed with the Manly preference index (Manly, 1974) using the following formula:

$$\beta_1 = \frac{\log e_1/A_1}{\log e_1/A_1 + \log e_2/A_2}$$

where β_1 is the index of preference for *E. formosa* pupae, e_1 is the number of surviving *E. formosa* pupae, e_2 is the number of surviving *T. vaporariorum* nymphs, A_1 is the initial number of *E. formosa* pupae and A_2 is the initial number of *T. vaporariorum* nymphs. The Manly index can take values between 0 and 1, with $\beta < 0.5$ indicating no preference for the parasitoid.

Greenhouse experiment

For the statistical analysis, the number of fourth instar whitefly nymphs was averaged per cage. This value of *T. vaporariorum* nymphs/cage was compared among treatments with a generalized linear model using Rstudio (version 2022.0.2.485). We used the function generalized least squares of the linear and nonlinear mixed effects models (Gaussian family and identity link function). The data were normalized using the Box-Cox transformation. Means were separated using Tukey's multiple comparison test (emmeans package).

To establish the effect of the predator on the parasitoid, the abundance of pupae of *E. formosa* per cage was compared between the 'Ef' and 'combined' treatments using a generalised linear model. Similarly, the abundance of *T. cucurbitaceus* nymphs and adults per cage was compared between the 'Tc' and 'combined' treatments to quantify the effect of the parasitoid on the predator.

Results

Non-choice experiment

T. cucurbitaceus females preyed on both *T. vaporariorum* nymphs and *E. formosa* pupae. However, consumption was significantly higher ($F_{1,28} = 4.49$; $P = 0.043$) on non-parasitized (33.33 ± 1.96) than parasitized nymphs (24.04 ± 3.93).

Free-choice experiment

Similar results were observed in the free choice experiment where the predator consumed an average of 13.20 ± 1.78 non-parasitized whitefly nymphs and 4.84 ± 0.89 *E. formosa* pupae ($P < 0.0001$). Manly preference index was $\beta = 0.24$ indicating that *T. cucurbitaceus* preferred to prey on fourth instar whitefly nymphs over *E. formosa* pupae.

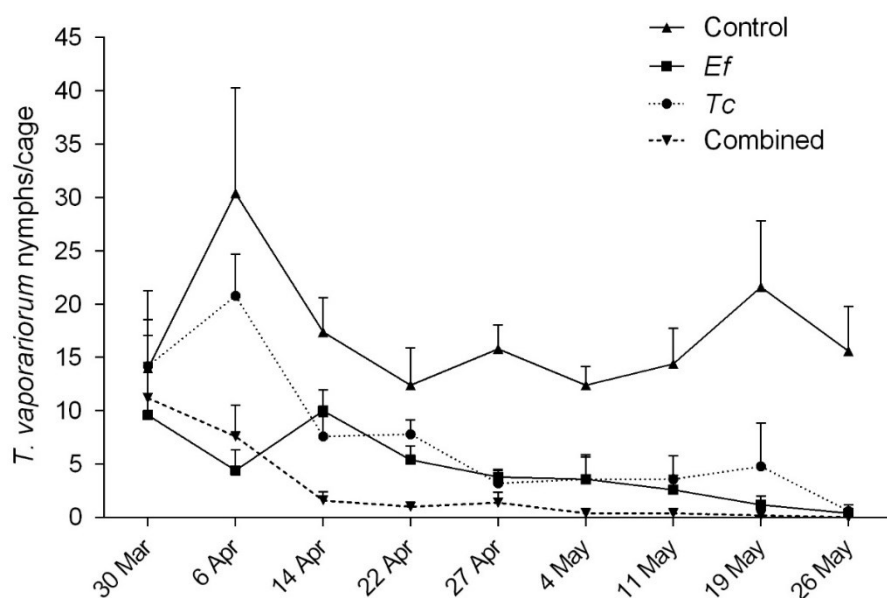


Figure 1. Mean (\pm SE) abundance of *T. vaporariorum* fourth instar nymphs per cage in each treatment during the experiment. 'Ef': *E. formosa* alone; 'Tc': *T. cucurbitaceus* alone; 'Combined': *E. formosa* + *T. cucurbitaceus*.

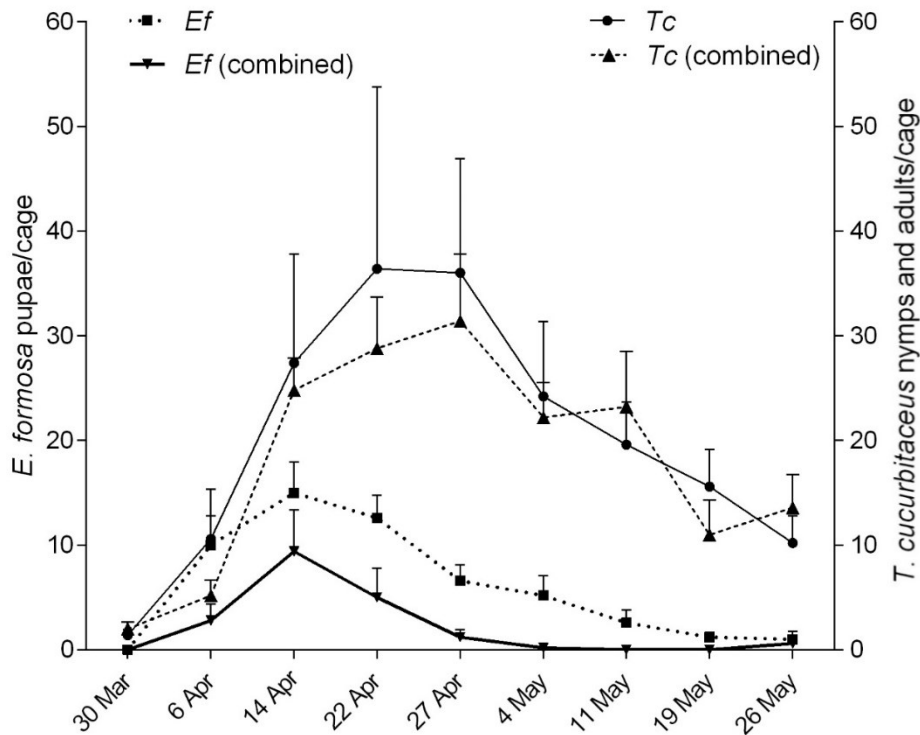


Figure 2. Mean (\pm SE) abundance of *T. cucurbitaceus* nymphs plus adults per cage (right axis) and mean (\pm SE) abundance of *E. formosa* pupae (left axis) in ‘alone’ and ‘Combined’ treatments. ‘Ef’: *E. formosa* alone; ‘Tc’: *T. cucurbitaceus* alone; ‘Ef (combined)’: *E. formosa* in the combined treatment; ‘Tc (combined)’: *T. cucurbitaceus* in the combined treatment.

Greenhouse experiment

During the course of the greenhouse experiment, a mean temperature range (\pm SD) of $15.8 - 29.5 \pm 3.9$ °C and a mean relative humidity range (\pm SD) of $49.0 - 66.5 \pm 4.2$ % were recorded.

The abundance of *T. vaporariorum* nymphs was affected by the presence of *T. cucurbitaceus* and *E. formosa* ($F_{3,128} = 31.11$; $P < 0.001$) (figure 1). At the beginning of the experiment (March 30th 2022), whitefly abundance was similar among the 4 treatments ($P > 0.05$). When natural enemies were released alone (‘Tc’ and ‘Ef’ treatments) a significantly lower whitefly abundance was recorded, compared to the control from May 11th until the end of the experiment ($P < 0.05$). On the other hand, this effect on pest population was observed earlier, from April 14th, in the ‘combined’ treatment ($P < 0.05$). No differences were registered between ‘Tc’ and ‘Ef’ treatments throughout the experiment. Moreover, no differences were detected between the ‘combined’ treatment and the natural enemies released alone, except on specific dates (April 14th: ‘combined’ vs ‘Ef’, $P = 0.018$; April 22nd: ‘combined’ vs ‘Tc’, $P = 0.025$; May 4th: ‘Ef’ vs ‘combined’, $P = 0.021$).

An asymmetrical interaction between natural enemies was observed when they were released together. The presence of the parasitoid did not have a significant effect on predator abundance ($P = 0.18$) (figure 2). Nymphs and adults of the predator were recorded throughout the experiment; its abundance increased progressively until a maximum (22 and 27 April) and then decreased accompanying the fall on pest population (figure 2). In contrast,

the presence of the predator had a significant effect on *E. formosa* abundance ($P < 0.002$).

In both treatments, ‘Ef’ and ‘combined’, *E. formosa* pupae were recorded for the first time on April 6th and reached their maximum abundance the following week (April 14th). In the ‘alone’ treatment *E. formosa* population decreased progressively. However, when it was released together with the predator it decreased more abruptly, reaching zero values towards the end of the experiment (figure 2).

Discussion

It is possible to observe the coexistence of *T. cucurbitaceus* and *E. formosa* in Argentinian tomato crops under greenhouse conditions. This is because the introduction of the mirid to control *T. vaporariorum* demands a restricted use of insecticides, favouring the spontaneous colonization of the aphelinid parasitoid (Polack *et al.*, 2017). In the present work, for the first time, the effect that the simultaneous presence of these natural enemies has on whitefly control was studied to estimate its potential as a control strategy.

In the simplified scenario of laboratory conditions, *T. cucurbitaceus* females engaged in intraguild predation on *E. formosa* pupae. The predator preferred parasitized over healthy nymphs in a ratio of 0.72 when *E. formosa* was the only prey available. However, when the prey was available, the predator preferred healthy *T. vaporariorum* nymphs and thus the previous ratio decreased to 0.36.

Several authors have evaluated the acceptance of parasitized whiteflies nymphs as prey for hemipteran predators used in biological control. In laboratory experiments Castañé *et al.* (2004) observed that *Dicyphus tamaninii* Wagner (Hemiptera Miridae) and *Macrolophus caliginosus* Wagner (Hemiptera Miridae) have a marked tendency to avoid *E. formosa* pupae, while they showed no preference for this prey in greenhouse samples. *Macrolophus pygmaeus* Rambur (Hemiptera Miridae) also preferred to consume non-parasitized *B. tabaci* nymphs when offered along with *Eretmocerus mundus* Mercet (Hymenoptera Aphelinidae) larvae (Malo *et al.*, 2012). It was suggested that a hardening of the host cuticle as the parasitoid develop within the nymph might explain the preference of some predators for healthy whiteflies (Castañé *et al.*, 2004). In contrast, other hemipterans preferred to consume parasitized nymphs. *Orius majusculus* Reuter (Hemiptera Anthocoridae) (Sohrabi *et al.*, 2013) had a clear preference for parasitized over non-parasitized *B. tabaci*. The same result was observed for *Geocoris punctipes* Say (Hemiptera Lygaeidae) and *Orius insidiosus* Say (Hemiptera Anthocoridae) when offered a choice between pupal or larval parasitoid *Eretmocerus* sp. nr. *emiratus* and early fourth instar *B. tabaci* nymphs (Naranjo, 2007). This preferential predation on parasitized prey was associated with prey appearance, since hosts tend to swell and become opaque, or even black for *E. formosa* pupae, making it more apparent for foraging predators (Naranjo, 2007).

In the present work, *T. cucurbitaceus* preferentially preyed late fourth *T. vaporariorum* nymphs even when *E. formosa* is a more visually apparent prey. Presumably a mechanical constrains, such as the hardness of the sclerotized pupae, may be influencing predator choice.

It was also observed that some predators that avoid consuming pupae indiscriminately consume younger stages of the parasitoid (Hoelmer *et al.*, 1994). Further study will be necessary to assess if the age of the parasitoid has an effect on *T. cucurbitaceus* preference, or if the predator actively avoids preying on parasitized hosts by recognizing other changes associated with parasitism.

When the predators prefer non-parasitized prey, joint predator and parasitoid releases result in better biological control (Heinz and Nelson, 1996, Colfer and Rosenheim, 2001). Our greenhouse assay showed that both *T. cucurbitaceus* and *E. formosa* can reduce whitefly population when they are released individually, but this control is enhanced when released together, despite the negative effect that the predator has on parasitoid population. Even though *T. cucurbitaceus* prefers to consume non-parasitized whitefly nymphs it can also prey on parasitized ones, probably to a greater extent if they are in a state of recent parasitism contributing to reduce *E. formosa* population, although this has not been proven in this study. The wide range of prey documented for *T. cucurbitaceus* (López *et al.*, 2019) may also have contributed to the asymmetry of the interaction. Towards the end of the greenhouse assay, when the abundance of whitefly reached values near zero, *E. formosa* had no other resource to sustain its population and could not persist. In contrast, *T. cucurbitaceus* continued to be recorded, suggesting that it could have subsisted preying on other pests

developed in the cages (e.g. *T. absoluta* was detected, probably due to an initial infestation of the plants in the nursery). On the other hand, differences in foraging strategy have also been mentioned as negatively affecting *E. formosa* populations. Bennett *et al.* (2009) observed that *Dicyphus hesperus* Knight reduced the number and size of whitefly patches favouring its foraging strategy over that of the parasitoid. This mirid predator locates prey visually and probably *T. cucurbitaceus* does so in the same way, although this is only a conjecture. Instead, *E. formosa* searches its host by touch (van Lenteren *et al.*, 1976) so when the resource is scarce its competitive efficiency is reduced (Bennett *et al.*, 2019). An unexpected result was observed for the control treatment (whitefly alone) since its population remained stable over time. In the absence of natural enemies, it would have been expected a growth in the number of whitefly nymphs. Possibly the minimum temperatures recorded during the night influenced this result (average minimum temperature 8.6 ± 1.6 °C).

T. cucurbitaceus and *E. formosa* are able to reduce whitefly population when introduced separately. When introduced together they engage in a trophic interaction in which the predator feeds on immature stages of the parasitoid. As we hypothesised, our results showed that *T. cucurbitaceus* females are able to prey on *E. formosa* pupae. This intraguild predation interaction has a negative effect on the parasitoid population but not on the biological control of the pest population due to the feeding preference of *T. cucurbitaceus* for healthy whitefly nymphs. Given these results, we conclude that the simultaneous presence of *T. cucurbitaceus* and *E. formosa* contributes to an effective control of the whitefly population.

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